

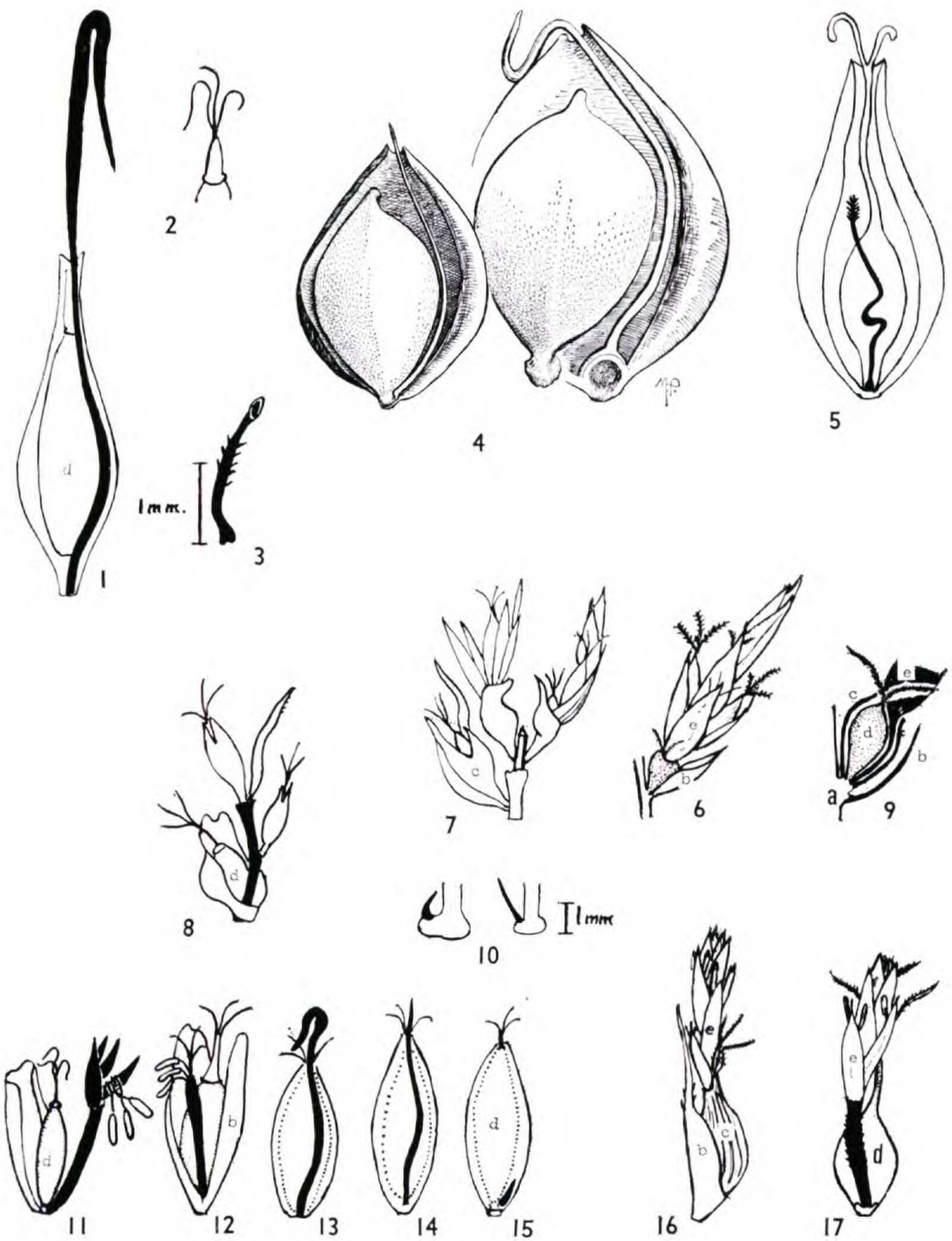
THE RACHILLA IN CAPE COD SPECIES OF CAREX WITH NOTES ON THE HISTORY OF THE PERIGYNIUM AND RACHILLA

HENRY K. SVENSON

This account takes up the local occurrence of the peculiar bristle-like or spikelet-bearing structure within the perigynium of *Carex*, known as the "rachilla". There is a review of various opinions, especially those of Duval-Jouve, Holttum, and Raymond. There is also a discussion of the relationship of *Cymophyllus* to *Carex* and to the West Indian *Bisboeckelera*. A plate with many figures illustrates the various interpretations of the rachilla.

It was a surprise to find on Cape Cod, in southeastern Massachusetts, *Carex* with development of the rachilla. First detected was *Carex Emmonsii*, which appeared peculiar to the naked eye. It grew in rich soil with skunk cabbage along the so-called Marston Mills River. The microscope showed that spikelets, developing within the perigynium, had extended out of it, a characteristic of *Schoenoxiphium*. This is a genus of sedges mainly South African. Further observation showed that this condition is not rare in *Carex Emmonsii* in dry sandy fields. *C. Emmonsii* is the commonest *Carex* on Cape Cod, and easily recognized by the tufts of long recurving leaves, which remain over winter. It grows especially well where the soil has been disturbed. The same rachilla structure is found, though less abundantly, in robust specimens of the closely related *Carex pensylvanica*. In a sandy field in Osterville, both species, together with rachilla-bearing *C. scoparia*, grew in a field being overrun by *Robinia viscosa*, *Prunus serotina*, and *Euonymus europaea*. Further good examples of *C. pensylvanica* were found in sandy fill near Johns Pond in Mashpee.

This axis within the perigynium assumes various forms, most commonly as a small bristle, but also as the schoenoxiphoid condition mentioned above (see fig. 7). On Cape Cod I have seen the rachilla in *C. scoparia*, *C. Swanii*, *C. debilis*



var. *Rudgei*, *C. bullata*, *C. canescens*, *C. Emmonsii* and *C. pensylvanica*. There are undoubtedly more. The figure of *C. complanata*, collected by me in Tennessee, was drawn by Miss Purdy about 1940. It has a rachilla reminiscent of a hookless *Uncinia*.

The rachilla in *Carex* was first noted by Kunth (1788-1850), who correctly interpreted it. The problem is illustrated in figs. 11-15, where rachillas are shown in the series *Schoenoxiphium* to *Carex*, based on figures from Kueken-thal (1909), *Das Pflanzenreich: Cyperaceae-Caricoideae*; and from R. S. Snell (1936). Anatomy of the spikelets and flowers of *Carex*, *Kobresia*, and *Uncinia*, in Bull. Torrey Club 63: 277-295. In *Carex*, as in fig. 15, the rachilla is commonly reduced; but see fig. 4, *C. complanata*, and fig. 5, *C. scoparia*. There are many examples in Boott's (1858), "Illustrations of the Genus *Carex*". In many of his illustrations the rachilla is flat with a serrated margin. That of *C. Fraseri* is strap-shaped without serrations. That of *S. scoparia* (my fig. 5) is perhaps closest to *C. Camposii* (t. 574) from the Sierra Nevada of Spain, which Kueken-

Figs. 1-17. The rachilla (except in 4) is black. Axis of spikelet, *a*; scale (glume), *b*; perigynium, *c*; achene, *d*. Fig. 1. *Uncinia uncinoides*, $\times 10$, Hawaii, Svenson, Sept. 5, 1960; 2. style-base enlarged. 3. Rachilla of *Carex tonsa*, Osterville, Mass., Svenson, June 10, 1967. 4. *Carex complanata*, $\times 10$, Altamont, Tennessee, Svenson, Oct. 3, 1935 (drawn by Maud H. Purdy). 5. *Carex scoparia*, $\times 10$, Osterville, Svenson 2933, June 23, 1970. 6. *Carex pallescens*, $\times 5$, from Duval-Jouve, pl. vii, f. 8. 7. *Carex Emmonsii*, $\times 5$, Svenson, June 16, 1967 (lowest scales removed). 8. Same collection as 7 (all scales removed). 9. *Carex pallescens*, $\times 10$, from Duval-Jouve, pl. vii, f. 9 (perigynium bisected longitudinally). 10. *Carex debilis* var. *Rudgei*, Osterville, Svenson, Aug. 18, 1967. 11-15. Diagrammatic sections to show rachilla of 11, *Schoenoxiphium*; 12. *Cobresia*; 13. *Uncinia*; 14. *Carex microglochin*; 15. *Carex* (with reduced rachilla); all from Snell (1936) and Kueken-thal (1909). 16. *Schoenoxiphium rufum*, $\times 6$, from C. B. Clarke, t. 141, f. 2. 17. The same, with perigynium removed, f. 3.

Dissections and samples of material from Cape Cod are filed on a sheet in the cover of *Carex Emmonsii* from Barnstable County in the herbarium of the New England Botanical Club.

thal places in the section *Elatae*, not represented in America. But none of Boott's plates illustrate a rachilla in the Ovales. By Barros (1935), Cyperaceae of Argentina, in *Anales Mus. Ciencias Nat. Hist.*, the rachilla is shown in 4 species.

The best account of these contradictory structures is by Duval-Jouve (1864): *Sur la signification morphologique d'une anomalie que présentent les utricules de quelques Carex*, in *Bull. Soc. Bot. France*. 1864. 19 pp. 1 pl.¹ Since the structures are similar to those that I have found, and since many species treated by him are also in New England, I have given his account the most extended treatment. In the spring of 1864, Duval-Jouve first found *Carex pallescens* with peculiar compound spikes, and spikelets issuing from the perigynia. Altogether he records a list of 24 species with a rachilla, obtained from the vicinity of Arles and Strasbourg. The anomalous spikelets were found most frequently toward the base of the spike, sometimes in the middle (*C. acuta*, *C. pseudocyperus*, but only rarely toward the apex. In *C. flacca*², *C. Oederi*, *C. flava*, and *C. hirta*, compound spikelets were so abundant that in some localities it was almost impossible to find a plant without them. In *C. flacca* the rachilla appeared most often as the *Schoenoxiphium*-type. In *C. flava* the perigynia were often split,

¹N. J. Duval-Jouve (1810-1883). For biography see Flahault, *Bull. Soc. Bot. France*. His work is typical of the best of French botanists. He is perhaps best known for his work, illustrated in color, of *Equisetum hiemale*. All is as though inlaid with gold. His work on *Carex* is equally as good. As a forerunner of botanical work he wrote a "Traite de Logique, ou Essai sur la theorie de la Science", Paris (1848), and a second edition, which I have seen, in 1885. It treats of various kinds of observations, perceptions, evidence, etc., things which often today tend to be forgotten. Surely no other botanist was so well prepared for his scientific task. I did not, however, find a history of the transition of nomenclature from logic to biology, in which I was particularly interested.

²Now a very abundant and variable species throughout the gypsiferous region (about Windsor), often growing in grassy pastures near the gypsum cliffs. Roland, *Fl. Nova Scotia* (1947), p. 230.

resembling *Elyna spicata*. All species were in places highly modified by pastures, ditches, animals, and in many other ways. They were best developed on terrain newly disturbed, or where traces of modification were apparent. On Cape Cod, *Carex pallescens*³ is common in grassy places, but I have yet to find a specimen with a rachilla.

The achene in *Carex* represents the lowest element of a reduced axillary inflorescence, and the achene occupies a basal lateral position at the lower part of the perigynium. This axis (the rachilla) when present is commonly bristle-like, or it may have several flowers as in *Schoenoxiphium*. Presence and development of the rachilla and the origin of the perigynium have been the subject of intensive study — one of the unfilled crossword spaces in the Cyperaceous organization. It is generally conceded that the perigynium consists of a single scale, and not the union of two scales. Torrey, in *North American Cyperaceae* (1838), p. 404, noted in a specimen of *C. Willdenowii* that the perigynium of the lowest flower enclosed the peduncle of a separate staminate spike. The two remaining pistillate flowers had within the perigynium, in place of a staminate spike, a green squamaceous rudiment. "This curious plant, therefore, seems in a manner to connect *Schoenoxiphium* N. ab E. with *Uncinia*, and to explain the nature of the setaceous body in the latter genus".

Theodore Holm (1854-1932) provides a bibliography of 55 items on the perigynium, together with an excellent account of terminology, in *Am. Journ. Sci. ser. II.* 214-220 (1896) entitled "The cladoprophyllum and anthopro-

³The var. *neogaea* Fernald (*Rhodora* 44: 306. 1942) is supposed to be without a short beak at the apex of the perigynium; but Boott (1858, pp. 39, 40) says the beak may be present or absent, and he shows a beak in t. 450, illustrating a specimen from Rhode Island. Kuekenenthal (1909, p. 433) describes the perigynium as erostrate except in var. *glaberrima* which has "utriculae interdum brevissime rostratae". The American var. *neogaea* therefore does not appear to amount to much. On Cape Cod, and otherwise in Massachusetts as I have seen it, *Carex pallescens* does not have the appearance of a native species.

phyllum in *Carex*", and the accompanying plate shows schoenoxiphoid spikelets in *C. crinita* and *C. Sprengelii*. Holm was one of the ablest of American botanists, who combined precise taxonomy with morphology; he was also an excellent artist. One of the latest accounts is by Holttum: "The spikelet in Cyperaceae" in Bot. Review, vol 14 (no. 8) 525-541. 1948. He, likewise, reviews the history of the perigynium. Much of the interest in the subject comes from the fact that *Carex* is one of the world's largest genera, and because it is abundant in the north temperate region. 267 species are listed in Gray Man. ed. 8; 793 species in Kuekenenthal's world-wide treatment (1909).

The development of the perigynium is almost like a second evolution of the seed plants. The developing embryo has been protected within the perigynium. Dispersal of mature perigynia is by floating, flying, attachment to men or animals, or in many other ways. This protection has emancipated *Carex* from the tropics, which (according to Holttum and to Raymond) is its primitive home, and allowed its penetration into areas freed from the Pleistocene ice. Raymond (1959): *Carices indochinenses necnon siamenses*. Mém. Jard. Bot. Montreal, no. 53, mentions the *Careyanae* and *Pandophyllae* as perhaps the most primitive elements of *Carex*. The *Careyanae* were segregated by him from the *Laxiflorae*, which are characteristic sedges of the Appalachian forest of southeastern United States.

As Fernald says (Rhodora 5: 249. 1903) the genera of the *Cariceae* are not very good: "Besides the genus *Carex* the members of the *Cariceae* have been grouped by different modern authors into various ill-defined genera varying with the personal equation". But that is also true of other genera in the Cyperaceae. The presence of the rachilla in widely diverse species of *Carex* led Duval-Jouve to suspect that the rachilla might not be of phylogenetic significance, but merely atavistic remnants appearing sporadically. Thus the occurrence of the rachilla in many species of *Primocarex* led to the early idea that *Primocarex* was prim-

itive. It is interesting in this respect to compare the rachilla of *C. complanata* (fig. 4) with *Uncinia* (fig. 1).

Of interest is the lack of an articulation or joint in the style of the *Vesiculares* (in which the perigynium is highly adapted for floating), and in the *Ovales*⁴ (in which it is wind-distributed). The *Ovales* have their great distribution on the Atlantic coastal plain and in Pacific North America, cf. chart by Kuekenthal (1909) p. 14, and the recent fine treatment by Hermann (1970): "Carices of the Rocky Mountains and Colorado Basin". Nelmes: "Facts and Speculations on phylogeny in the tribe Cariceae" in Kew Bull: (1961) 427-436, explained that some unispicate species were of uncinoid origin, and he distributed most of Kuekenthal's *Primocarex* variously in the genus. And to emphasize the ill-defined genera, Kuekenthal (1940) described *Schoenoxiphium kobresioides* from material collected by Van Steenis in Sumatra, and termed it the "Verbindungslied zwischen *Schoenoxiphium* und *Kobresia*".

Holttum thought *Mapania* to be the most primitive genus. See also my comments on *Mapania macrophylla* in Bull. Torr. Club 75: 95. 1948, with fig. 3. The breakdown of the tubular translucent corolla provides us with a possible origin of the perigonial bristles in the *Cyperaceae*. I was incorrect in ascribing *M. macrophylla* to Santo Domingo as well as British Guiana. Meyer's plants all came from the Essequibo River in British Guiana.

Mackenzie set up *Cymophyllus*, based on *Carex Fraseri*. By Pursh it was considered a *Mapania*, but I believe it to be a true *Carex*, illustrated by Boott (t 484) with a strap-shaped rachilla. There is a reduction series in the West Indies from *Mapania* and *Hypolytrum* to *Bisboeckelera* (*Hoppia*) and *Calyptracarya*, which simulates *Carex*; but I think it is an unrelated parallel series, as shown by the various illustrations in Clarke's "Illustrations of Cypera-

⁴The style is said to be jointed by Mackenzie, and is so illustrated in North American Cariceae (1940), but I have not found it so. See fig. 5).

ceae" (1909). In my illustration of *Mapania sylvatica*, the type of the genus, in "Cyperaceae of Panama", the corolla segments are inrolled around the stamens. This I am sure is the correct interpretation, and the flower is a normal flower of the Cyperaceae, and not an assemblage of "partial inflorescences". (Ann. Missouri Bot. Gard., 1943)

Another interesting structure in *Carex* is the style-base, which is sometimes swollen and articulated. Duval-Jouve described *C. oedipostyla*, i.e. with a "swollen foot" in Mém. Acad. Sci et Lettres de Montpellier (1870), including a plate with many figures. The articulating style-base is widespread in *Eleocharis* and some other genera, but has little real significance in their delineation. It is one of the historical straws grasped by the drowning botanist. Some decades ago I thought that the swollen style-base in the *Laxiflorae* might be a transition to broadleaved *Cyperus* (*Mariscus*) of the tropical rain forest, and especially to *Cyperus diffusus*. The structure of the achene and prophyllum in *Carex* (including perhaps *Schoenoxiphium*), is closer to *Cyperus* than to any other genus. In visiting Nicaragua last spring, I found *Cyperus diffusus* to be a roadside and plantation weed, and not a rain forest type. It is probably different in the Old World.

Schoenoxiphium is generally considered to be the most primitive of the *Caricoideae*, and the accompanying figures from Kuekenthal, Snell, and Clarke show the ideas presented. It is a small genus centering on South Africa, and extending to the mountains of Madagascar, southern Siberia just north of Afghanistan (Krechetovich in Flora Tadzhikskoi USSR 2: 10-12. 1963), and to Sumatra. D. M. Napper, in Journ. East Afr. Hist. Soc. and Corydon Museum, Nairobi, 24 (no. 2); 1963, p. 12, says "predominantly South African, about 15 species. The normal habitats are damp forests and wooded or open grasslands. It is unusual for *Schoenoxiphium* to occur at the higher altitudes (over 7,000 or 8,000 ft.) where *Carex* usually occurs".

The *Caricoideae* include *Schoenoxiphium* Nees (1832), *Kobresia*⁵ Willd. (1809), *Elyna* Schrader (1806), *Uncinia* Persoon (1807), and *Carex*⁶ Linnaeus (1753).

Kobresia has according to Kuekenenthal (1909) its origin and central point in the high mountains of central Asia from Turkestan to Central China. 14 of the species are peculiar to the Himalayas, especially the western part, and 5 to the high mountains of Central China. The few North American species are well treated (with photographs) by Dunan in Bull. Torrey Club 83: 192-195. 1956; and in *K. simpliuscula* rachillas are shown. According to Mackenzie, *Kobresia* extends from Newfoundland and Greenland to Colorado and Alaska. *K. elachycarpa* Fernald was described in 1897 from banks of the Aroostook River at Fort Fairfield in Maine, but later treated by him as *Carex elachycarpa*, which goes to show how tenuous are the limits of these genera.

Uncinia has been well treated by Kuekenenthal (1909) and consists of 24 species mainly of the southern hemisphere from the Antarctic Islands through the South American Andes to Mexico and Jamaica. The remainder is in Australia, Tasmania, New Zealand, New Guinea, and the Hawaiian Islands. The illustrated specimen (fig. 2) was collected by me in the Hawaiian Islands.

Carex microglochin Wahlenberg is illustrated in fig. 4. It extends from Greenland to Alaska, southward to Quebec and Colorado. It is also known in the Patagonian region and in Eurasia. In describing the occurrence in Newfoundland, Fernald in Rhodora 28: 61. 1926, says "It is one of the rarest and taxonomically most interesting of species, having the primitive rachilla, which is obsolete in most

⁵According to Kuekenenthal, named for the botanophile Paul de Cobres of Augsburg. It is sometimes spelled with a "C".

⁶Duval-Jouve (1864, footnote p. 16): The word *Carex* was used by Virgil, Columella, Calpurnia, etc., to designate hard, sharp, or cutting herbs . . . perhaps tall *Juncus*, *Typha*, or *Sparganium*, or perhaps dry thickets at the borders of pastures, i.e. "Fronibus hirsutis et carice pastus acuta" thickets which the shepherds of Provençal still call *carigues*.

northern *Carices*, projecting from the top of the perigynium; in other words, *C. microglochin* is an excessively local relic-species now known only in a few remote corners of the globe, and about as well placed in the Antarctic genus *Uncinia* as in the genus *Carex*, which abounds in the northern hemisphere . . . its prickly little fruit had obviously been spread by pedestrians with their high skin boots."

Now, with all these contradictory views, and the questionable relationship of the various elements, it is hoped that the reader will go out to collect some rachilla material for himself, and will then turn to Fernald's amusing story of *Carex microglochin* in the twenty-eighth volume of *Rhodora*.

OSTERVILLE, MASSACHUSETTS 02655